E-Article

Interspecific Dominance Via Vocal Interactions Mediates Altitudinal Zonation in Neotropical Singing Mice

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abstract: Interspecific aggression between ecologically similar species may influence geographic limits by mediating competitive exclusion at the range edge. Advertisement signals that mediate competitive interactions within species may also provide social information that contributes to behavioral dominance and spatial segregation among species. We studied the mechanisms underlying altitudinal range limits in Neotropical singing mice (*Scotinomys*), a genus of muroid rodent in which males vocalize to repel rivals and attract mates. We first delineated replacement zones and described temperature regimes on three mountains in Costa Rica and Panama where Chiriquí singing mice (*S. xerampelinus*) abruptly replace Alston's singing mice (*S. teguina*). Next, we conducted interspecific behavioral trials and reciprocal removal experiments to examine if interspecific aggression mediated species replacement. Finally, we performed reciprocal playback experiments to investigate whether response to song matched competitive interactions. Behavioral trials and removal experiments suggest that *S. xerampelinus* is behaviorally dominant and excludes *S. teguina* from higher, cooler altitudes. Playback experiments indicate that subordinate *S. teguina* is silenced and repelled by heterospecific song, whereas *S. xerampelinus* responded to heterospecifics with approach and song rates comparable to responses to conspecifics. Thus, interspecific communication reflects underlying dominance and suggests that acoustic signaling contributes to altitudinal zonation of ecologically similar congeners. Our findings implicate the use of social information in structuring spatial distributions of animal communities across landscapes and provide insight into how large-scale patterns are generated by individual interactions.

Keywords: acoustic communication, altitudinal replacement, interspecific aggression, reciprocal playback, social information, species interactions.

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Introduction

Competition for limited resources often results in the evolution of displays that minimize direct physical combat (Maynard Smith and Harper 2004). In many species, signals reduce escalation of aggressive contests by conveying information about resource-holding potential (Parker 1974) to a network of potential competitors over long distances (Bradbury and Vehrencamp 1998). While trait-mediated indirect interactions are known to strongly influence spatial and community dynamics in other contexts (e.g., predator-prey systems; Bolker et al. 2003; Werner and Peacor 2003), the role of competitive signaling in structuring animal communities is less understood.

Signals used to resolve conflicts within species can also be an important component of aggression between species (Bradbury and Vehrencamp 1998; Ord and Stamps 2009; Goodale et al. 2010; Peiman and Robinson 2010). In particular, advertisement vocalizations that mediate competitive interactions among conspecific males may also contribute to interspecific dominance and territoriality when ecologically similar species come into contact (Orians and Willson 1964; Murray 1981; Catchpole and Leisler 1986; Gerhardt and Huber 2002). In birds, response to heterospecific signals reflects underlying dominance interactions; subordinate species are silenced and/or repelled, whereas dominant species respond aggressively (Robinson and Terborgh 1995; Martin et al. 1996). At small spatial scales, this type of asymmetric vocal dominance can result in local habitat segregation (Martin and Martin 2001*a*, 2001*b*). At broader scales, interspecific communication may facilitate competitive exclusion of subordinate taxa across environmental gradients (Robinson and Terborgh 1995). Acoustic signaling thus represents an important yet understudied mechanism mediating interspecific aggression that may contribute to spatial segregation at species limits.

The abrupt replacement of species along altitudinal gra-

dients has long fascinated biologists (von Humboldt 1807; Merriam 1895; Shreve 1915, 1922) and provided an opportunity to study how biotic factors limit geographic distributions (Brown 1971; Heller 1971; Hairston 1980; Repasky and Schluter 1994;). Interspecific competition is posited to be a major factor delimiting the range edge of closely related parapatric species (Bull 1991), though most evidence is based on expansion of altitudinal ranges in the absence of putative competitors (Lack and Southern 1949; Terborgh and Weske 1975; Mayr and Diamond 1976; Remsen and Graves 1995) where abiotic regimes are assumed equivalent (Cadena and Loiselle 2007). However, more recent experimental work in Neotropical birds suggests that interspecific aggression maintains altitudinal range margins (Jankowski et al. 2010), highlighting the importance of behavioral interactions in limiting species distributions.

Neotropical singing mice (*Scotinomys*) are diurnal, insectivorous rodents distributed throughout the mountains of Middle America. Alston's singing mouse (*Scotinomys teguina*; 9–12 g) is a widespread species inhabiting mid- to high-altitude cloud forest, forest edge, and abandoned pastures from southeastern Mexico to western Panama (1,000–2,900 m), whereas the Chiriquí singing mouse (*Scotinomys xerampelinus*; 13–15 g) is restricted to the highest forested summits and páramo of Costa Rica and Panama (2,200–3,300 m; Wilson and Reeder 2005; Hooper and Carleton 1976; fig. 1). The two ecologically similar congeners occupy parapatric distributions in the Cordillera de Talamanca and Cordillera Central, where the upper

Video 1: Still photograph from a video (video 1) available in the Dryad Digital Repository. Vocal response of a male Alston's singing mouse (*Scotinomys teguina*) to playback of conspecific song.

distribution of *S. teguina* contacts the lower distribution of *S. xerampelinus* between 2,200 and 2,900 m (Enders and Pearson 1939; Hooper 1972; Hooper and Carleton 1976; herein). Interspecific competition and species differences in thermal tolerance are hypothesized to maintain this narrow contact zone (Hill and Hooper 1971; Hooper and Carleton 1976). Males of both species commonly sing species-specific trills (Miller and Engstrom 2007; Campbell et al. 2010) that are modulated by androgens and used in mate attraction and male-male aggression (Pasch et al. 2011*a*, 2011*b*, herein; video 1, available in the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.v43b8). Vocalizations of *S. teguina* are long (4–7 s), de-

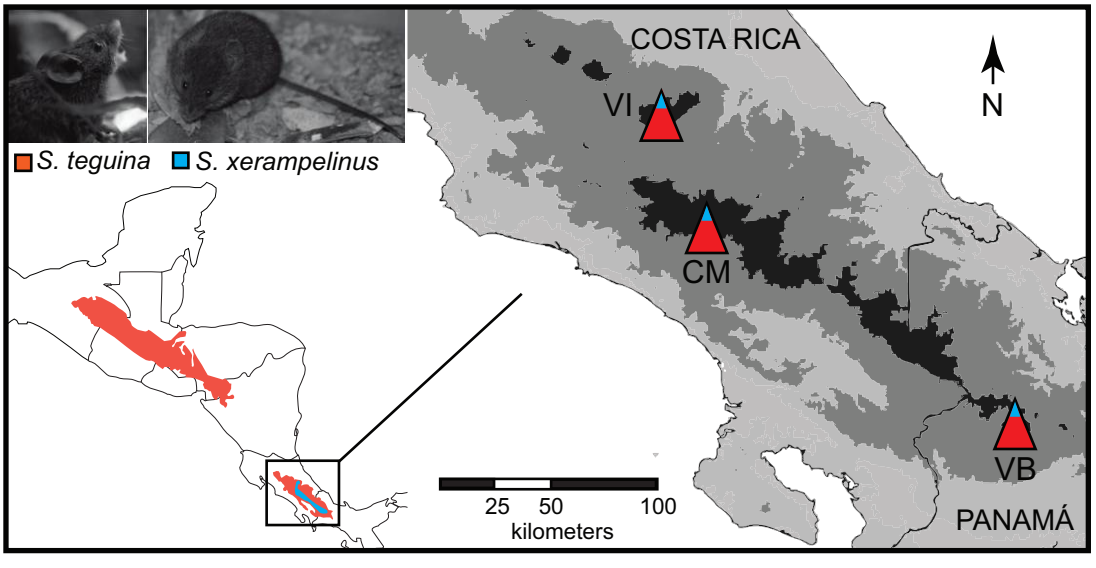


Figure 1: Latitudinal and altitudinal distributions of Neotropical singing mice (*Scotinomys*). *Scotinomys xerampelinus* (blue) replaces *S. teguina* (red) on the highest mountains of Costa Rica and Panama. VI = Volcán Irazú, CM = Cerro de la Muerte, VB = Volcán Barú.

celerating trills with high dominant frequencies (22–26 kHz), whereas *S. xerampelinus* trills are shorter (1–2 s) and lower in frequency (16–20 kHz: Campbell et al. 2010; audio files 1 and 2, available online in the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.v43b8; Pasch et al. 2013).

The first goal of this study was to identify the altitude of species replacement along three slopes in the Cordillera de Talamanca and Cordillera Central. We placed data loggers at replacement zones to determine the contribution of temperature in limiting species distributions. Similar temperature regimes at replacement zones on different mountains would suggest that abiotic factors are important in limiting one or both species. Our second goal was to evaluate whether interspecific interactions, corresponding to physical contact and/or communication between individuals of different species, influenced altitudinal range limits. If behavioral interactions mediate species replacement, we predicted that (*a*) species would exhibit interspecific aggression in staged behavioral trials and (*b*) removal of one species would result in competitive release of the opposite species (Connell 1983). Finally, if interspecific vocal interactions contribute to altitudinal zonation, we predicted that behavioral responses to playback of heterospecific song would reflect species differences in behavioral dominance.

Methods

Altitudinal Replacement Zones and Temperature Regimes

In June–August 2007, we established trapping transects to demarcate zones of altitudinal replacement on two mountain slopes in Costa Rica (Cerro de la Muerte [CM], Volcán Irazú [VI]) and one slope in Panama (Volcán Barú [VB]; fig. 1). Hooper and Carlton's (1976) original account of contact zones guided the selection of study sites. A 200 × 30-m grid of 44 traps (spaced 20 m perpendicular and 10 m parallel to the cline, respectively) was placed in the understory for 20 days at each site. If *Scotinomys teguina* was captured, the entire grid was moved 50 m upslope the following day. In addition, sporadic trap lines were placed at altitudes ±300 m from the trapping grid to validate species distributions. Sherman live-traps (model SFA) were baited with peanut butter and oats and checked daily. We defined the altitude of replacement as the trapping grid where *Scotinomys xerampelinus* was captured and *S. teguina* was not captured over the course of 5 trap days.

We placed temperature loggers (Hobo Pendant, model UA-001-64, Onset Computer) in the understory at replacement zones to collect ambient temperature every hour for 1–3 years to provide a general estimate of ambient temperatures experienced by each species. At one site (VI), we placed a temperature logger at the top of the mountain to characterize temperature regimes where *S. xerampelinus* occurs in allopatry. Along the same slope, we estimated the lowest altitude of *S. teguina* occurrence by broadcasting conspecific song at 100-m altitudinal intervals. Response to song indicated species presence (Hooper and Carleton 1976). Broadcast songs were randomly selected from laboratory recordings of *S. teguina* captured higher on the same mountain (Campbell et al. 2010). We played stimuli at 54 dB SPL at 1 m from a Pioneer TS-250 speaker (flat frequency response 6–40 kHz) via an external sound card (Edirol FA-66) connected to a laptop running Adobe Audition. Songs were broadcast at 3-min intervals followed by 2 min of silence for 20 min between 0700 and 1000 hours. A temperature logger was placed at the lowest site where the vocal response of *S. teguina* was recorded.

Interspecific Behavioral Trials

We staged behavioral interactions between adult males of *S. teguina* and *S. xerampelinus* captured at the contact zone at CM and VI in June–August 2007 ($n = 9$ trials/site) to examine whether singing mice exhibited interspecific aggression. One individual of each species was placed on opposite sides of an 80 × 50 × 40-cm arena separated by an opaque partition for 48 h after capture. The arena was isolated in an open-air laboratory on site and animals were fed ad lib. with cat chow and water. The partition was removed between 0700 and 0900 hours to allow animals to interact for 10 min. We videotaped all trials and scored the number of aggressive attacks (chases and lunges) and latency to attack for each species.

Reciprocal Removal Experiment

If interspecific interactions mediate species replacement, we predicted that removal of one species would result in competitive release of the other species in the form of immigration. In May–August 2008, we performed a reciprocal removal experiment at the zone of replacement on VI, which coincided with a transition from secondary forest scrub (solely occupied by *S. teguina*) to primary forest (solely occupied by *S. xerampelinus*; appendix, available online). We established 12 32 × 24-m plots of 20 traps spaced 8 m apart in a rectangular grid. We paired control and removal plots for a given resident species (*S. teguina* or *S. xerampelinus*) with three replicates per species. Pairs of control-removal plots were spaced 100 m apart and were separated from all other paired plots by >500 m. The vertical distance between *S. teguina* and *S. xerampelinus* plots was about 30 m and spanned 15 m in altitude (fig. A1, available online). Trapping was conducted

for 3 consecutive days and every 5 days thereafter over 9 weeks. On control plots, resident animals were captured, marked for unique identification, and released on site. On removal plots, individuals of the resident species were captured, uniquely marked, and either used in laboratory playback experiments (below) or transplanted 2 km across a riverine barrier and never recaptured. Individuals of the colonizing immigrant species were uniquely marked and released on site. Temperature loggers were placed in the center of all plots to record temperature every hour for 14 days. Temperatures were averaged across control and removal plots for all replicates.

Field Playback Experiments

If vocal communication contributes to species replacement, we predicted that response to playback of heterospecific song would reflect underlying dominance interactions. During the removal experiment, we identified traps on control plots where resident males were captured most often. At the end of the experiment, we visited those trap sites ($n = 8$ per species) between 0600 and 1000 hours and waited 10 min before initiating playbacks. Three types of stimuli were played during each trial: control stimulus, heterospecific song, and conspecific song. Songs used in playback experiments were recorded from adult males of the same population during the previous year (Campbell et al. 2010). We selected at random two songs from each of eight males per species and used songs of a different male for each trial. Control stimuli were generated in Adobe Audition using band-pass-filtered white noise that matched the bandwidth, duration, and root mean square amplitude of corresponding conspecific songs. A Bruel and Kjær sound level meter (type 2219) and calibrator (type 4230) were used to calibrate the amplitude of stimuli to match average songs of *S. teguina* (54 dB at 1 m) or *S. xerampelinus* (63 dB at 1 m).

Each playback trial lasted 26 min and was recorded with a Sony PCM-50 digital recorder. We began with a 5-min prestimulus period to record baseline levels of singing. At 5 and 6 min we broadcast each of two heterospecific songs and recorded the number of songs evoked over a 5-min interval (7–12 min); at 12 and 13 min we broadcast each of two control stimuli and recorded responses for 5 min (14–19 min); and at 19 and 20 min we broadcast each of two conspecific songs and recorded responses from 21 to 26 min. In half of the trials, control stimuli were presented at 5 and 6 min and heterospecific stimuli at 12 and 13 min. Conspecific songs were always played last to avoid carryover effects that were apparent in preliminary studies (see Martin and Martin 2001*a*). Species identity of responding individuals was verified from analysis of digital recordings, with *S. teguina* songs being consistently longer than *S. xerampelinus* songs at VI (5.37 ± 0.95 s vs. 1.77 ± 0.41 s, respectively; Campbell et al. 2010).

Laboratory Playback Experiments

We used adult males captured on removal plots to perform playbacks in a controlled laboratory setting to quantify animal movement associated with vocal responses. Animals were housed singly in 28 × 28 × 28-cm PVC-coated wire mesh cages and isolated in anechoic chambers for 24 h before we initiated trials between 0600 and 1000 hours. Individuals of each species were assigned randomly to playback of one of three stimuli: control stimuli, heterospecific song, or conspecific song (*S. teguina*: $n = 8$ per treatment; *S. xerampelinus*: $n = 5$ per treatment). We selected three songs from each of four individuals of each species from laboratory recordings of the same population (Campbell et al. 2010). Control stimuli were synthesized by generating white noise bounded within species-specific bandwidths (*S. teguina*: 10–42 kHz, *S. xerampelinus*: 10–38 kHz). We played stimuli at 50 dB SPL at 1 m from one of four randomly selected Pioneer TS-250 speakers placed on each side of the mesh cage. Mice were recorded for 20 min to obtain prestimulus song rate. At 20, 21, and 22 min, we broadcast one song followed by 2 min of silence. The sequence was repeated three times with songs from different males. For control treatments, the single control stimulus was broadcast at the same rate as conspecific and heterospecific song treatments. We recorded the total number of songs emitted by focal animals in the 20-min period following the initial stimulus. We also calculated the amount of time animals spent on the side of the cage that held the speaker emitting the stimulus.

Statistical Analyses

We analyzed response to the removal experiment using a Poisson generalized linear mixed model fit by a Laplace approximation (Bolker et al. 2009). Explanatory variables included treatment (control vs. removal), species identity of resident animals (*S. teguina* or *S. xerampelinus*), species identity of colonizing animals (*S. teguina* or *S. xerampelinus*), and plot replicate coded as a random effect.

To analyze response to reciprocal playback experiments in the field, we chose to fit a binomial ("sang" vs. "did not sing") rather than Poisson generalized linear mixed model (GLMM; "number of songs") because the number of songs was low (overall mean 0.69 songs/observation, 7/64 observations >1). We fitted both a binomial GLMM and a bias-reduced binomial generalized linear model. While in principle the block effect (ID) should be incorporated in the statistical model as a random effect to allow for the repeated-measures design, in practice its effect is

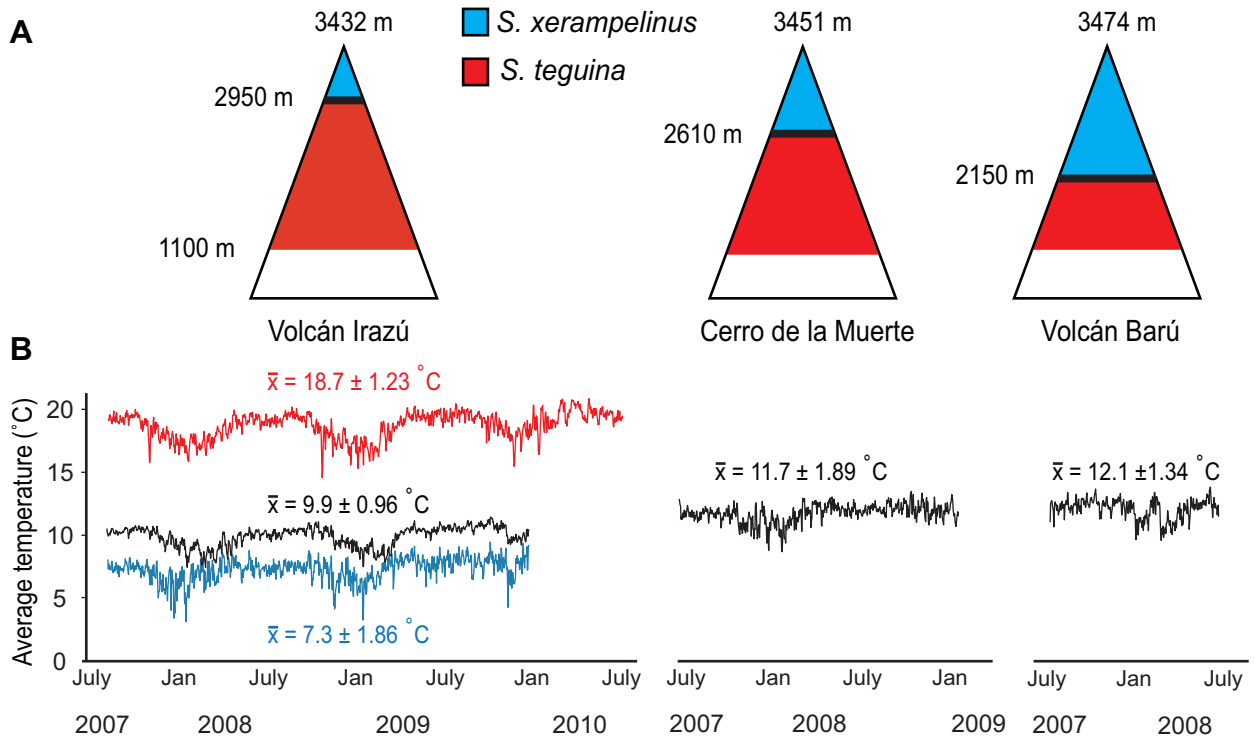


Figure 2: Altitudinal distributions and temperature regimes of Neotropical singing mice. *A*, Altitude of replacement (black line) on two mountains in Costa Rica (Volcán Irazú and Cerro de la Muerte) and one in Panama (Volcán Barú). *B*, Average temperature regimes at the site of replacement (black); Volcán Irazú, average temperature regimes of *Scotinomys xerampelinus* (blue) and *Scotinomys teguina* (red) in allopatry.

negligible (the among-individual variance in probability of singing is estimated as exactly zero). Dropping the block effect and treating the response as binomial allowed us to use bias-corrected logistic regression, which is more appropriate when (*a*) the sample size is small and (*b*) some categories have extreme values (e.g., *S. teguina* had zero instances of singing in response to heterospecific song). Order effects were statistically significant for neither species ($P > .5$) and were excluded from the model, resulting in stimulus type (control, conspecific, or heterospecific), species identity (*S. teguina* or *S. xerampelinus*), and their interaction as explanatory variables.

To analyze responses to playbacks in the laboratory, where songs were more frequent, we used a Poisson GLMM with stimulus type, species identity, and period (pre- vs. postplayback) as explanatory variables and subject coded as a random variable. Wald *z*-tests and Tukey's HSD-corrected post hoc comparisons were used to test for differences in responses among treatments. To test differences among treatment groups in the amount of time (s) spent near speakers, we used ANOVA followed by Tukey's test. All statistical analyses were performed in R using brglm v. 0.5–6 (Kosmidis 2007), lme4.0 v. 0.9999–2 (Bates et al. 2012), ggplot2 v. 0.9.0 (Wickham 2009), and multcomp v. 1.2–12 (Hothorn et al. 2008) for multiple comparisons–corrected *P* values.

Results

Altitudinal Replacement Zones

The altitude of replacement differed among mountains (VI: 2,950 m; CM: 2,610 m; VB: 2,150 m; fig. 2*A*), yet temperature regimes that characterized replacement zones were qualitatively similar (fig. 2*B*). Daily temperature profiles showed little variation and decreased with increasing altitude. Across their altitudinal distributions, *Scotinomys xerampelinus* experiences a narrower range and cooler temperatures than does *Scotinomys teguina* (*S. xerampelinus*: 7.3°–9.9°C; *S. teguina*: 9.9°–18.7°C; fig. 2*B*). On the mountain with the highest altitude of replacement (VI), the replacement zone was concomitant with a change in vegetation from early succession scrubland at lower elevations to mature forest at higher elevations (fig. A1). Such vegetation transitions were not readily apparent at other localities.

Interspecific Behavioral Trials

Scotinomys xerampelinus initiated more attacks than *S. teguina* in 17 of 18 trials (5.2 ± 0.9 and 0.67 ± 0.3 attacks, respectively; $t_{17} = 5.53$, $P < .0001$; fig. 3*A*). In the remaining trial, neither *S. teguina* nor *S. xerampelinus* exhibited aggression. Similarly, *S. xerampelinus* showed shorter latencies to attack than did *S. teguina* (158.9 ± 41.2 and 475.7 ± 49.6 s, respectively; Wilcoxon signed-rank = −67.5, $P < .001$; fig. 3*B*).

Reciprocal Removal Experiment

We trapped for 26,880 trap-hours over 9 weeks and captured 121 *S. teguina* (removed 65) and 71 *S. xerampelinus* (removed 34). *S. teguina* plots were warmer and showed more diel variation than *S. xerampelinus* plots (*S. teguina*: 11.5° ± 3.65°C; *S. xerampelinus*: 9.4° ± 0.78°C; Wilcoxon signed-rank test, −14,771, $P < .0001$; fig. 4*A*). While we did incorporate plot as a random effect in the model, the estimated among-plot variance was zero. We found no

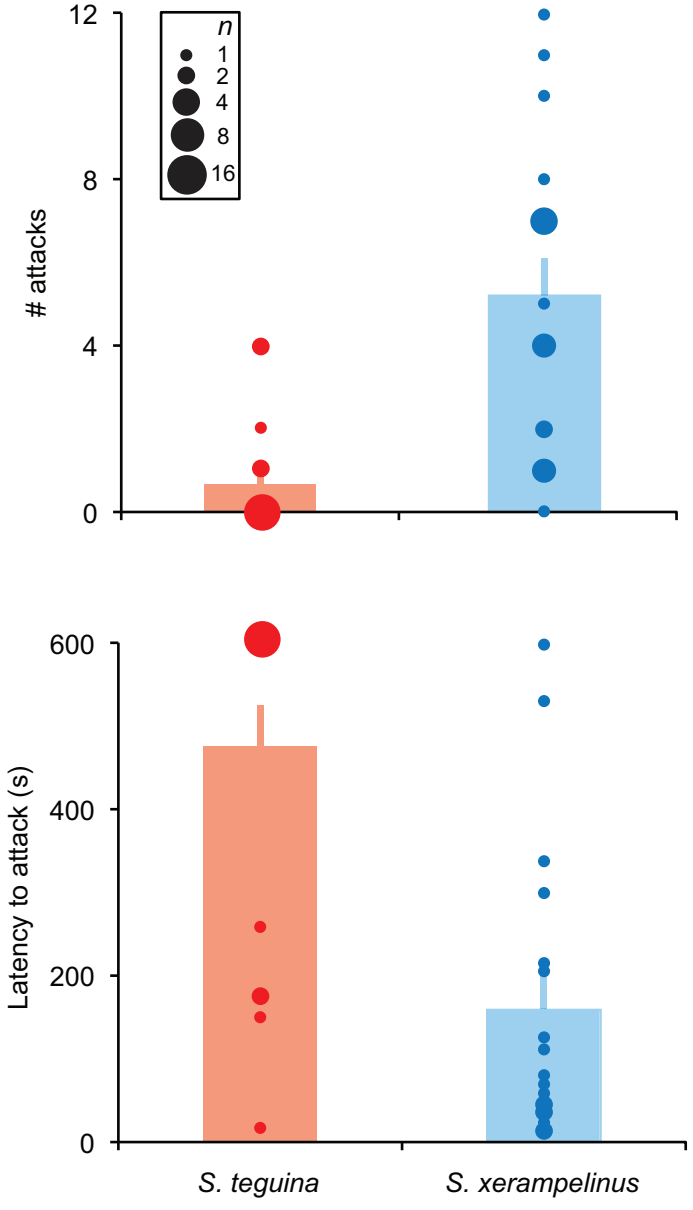
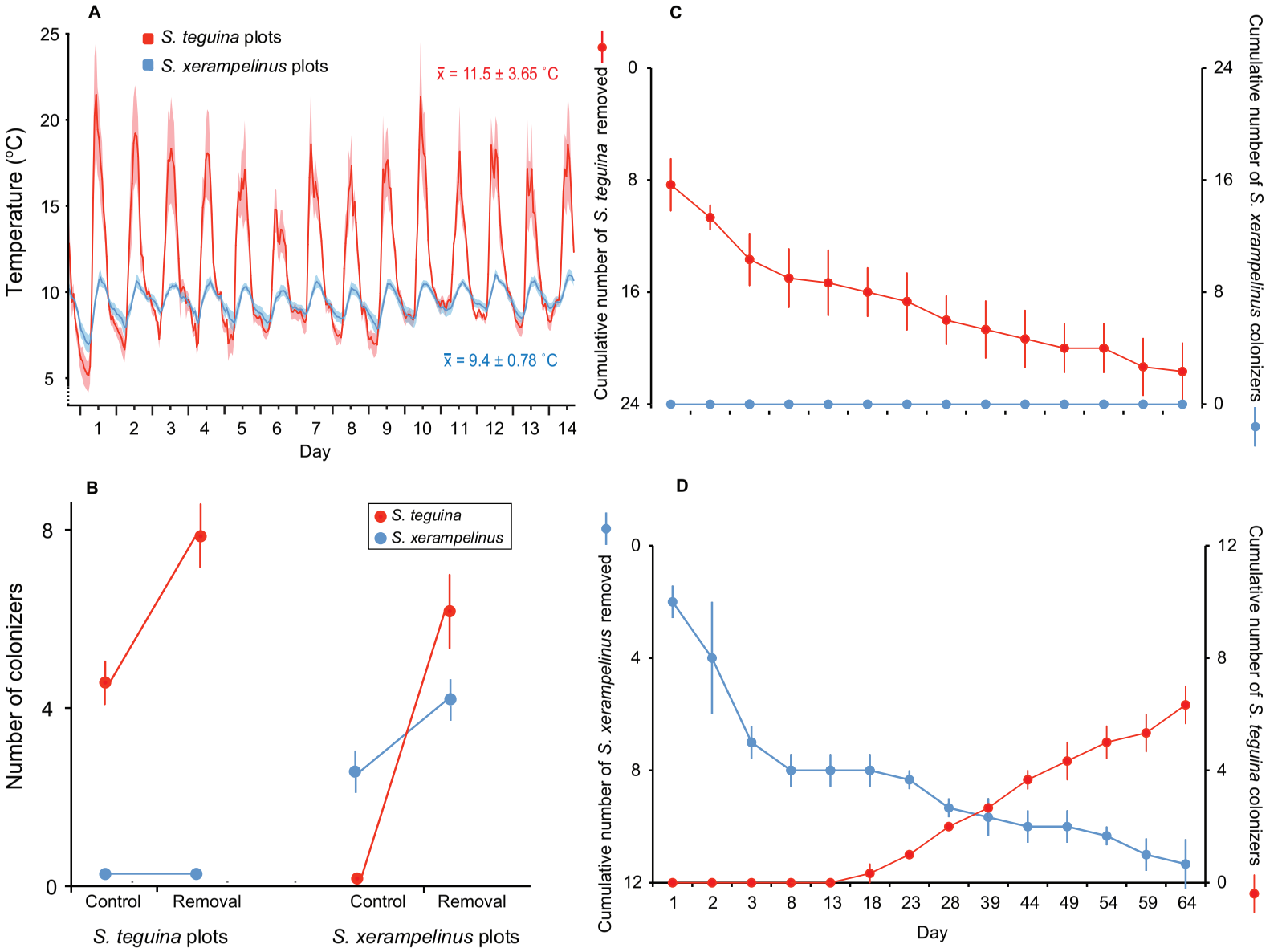


Figure 3: Interspecific aggression in Neotropical singing mice. *A*, Number of attacks initiated by both species during staged trials. *B*, Latency to attack by both species during staged trials in neutral arenas. Error bars are ±1 SE, $P < .001$.



species differences between the number of conspecifics colonizing control plots relative to removal plots where they occurred naturally (likelihood ratio test $\chi^2 = 0.01$, $P = .92$). However, we found an asymmetrical response on removal plots, indicated by a statistically significant interaction between resident species identity and the number of colonizing heterospecifics (likelihood ratio test $\chi^2 = 28.51$, $P < .001$; fig. 4*B*). *Scotinomys teguina* colonized *S. xerampelinus* removal plots within 3 weeks and remained there for the duration of the study ($n = 19$), whereas no *S. xerampelinus* colonized *S. teguina* removal plots (fig. 4*C*, 4*D*).

Field Playback Experiments

We found a statistically significant interaction between stimulus type and species identity (likelihood ratio test $\chi^2 = -19.1$, $P < .001$). Relative to control stimuli, *S. teguina* were more likely to sing in response to conspecifics (log-odds increase of 1.88) and less likely to respond to heterospecifics (log-odds decrease of 3.79); while neither change was individually statistically significant, the (multiple-comparisons-corrected) difference between the two responses was (Wald $z = 2.6$, $P = .03$; fig. 5*A*). Conversely, while *S. xerampelinus* showed a slight tendency to sing more in the response to experimental stimuli compared to control noise (log-odds increase of 1.41, Wald $z = 1.54$, $P = .12$), they did not differ in their response to conspecifics versus heterospecifics (Wald $z = 0.0$, $P = 1.0$; fig. 5*B*).

Laboratory Playback Experiments

As with the field playback experiments, we found a three-way statistically significant interaction between stimulus type, species identity, and period (likelihood ratio test $\chi^2 = 6.52$, $P = .04$). For *S. teguina*, an interaction between responses to conspecifics and heterospecifics post-treatment indicated that *S. teguina* were more likely to sing in response to conspecifics (log increase of 0.02) and less likely to respond to heterospecifics (log decrease of 1.37; Wald $z = -2.46$, $P = .014$; fig. 6*A*). Accordingly, *S. teguina* spent more time near the speaker broadcasting conspecific stimuli (73% ± 6%) and less time near heterospecific stimuli (12% ± 6%) compared to controls (44% ± 11%, $F_{2,21} = 14.45$, $P > .001$; fig. 6*B*). Conversely, while *S. xerampelinus* tended to respond more to experimental stimuli compared to control noise (log increase of 1.46, Wald $z = 1.64$, $P = .10$), they did not differ in their response to conspecifics versus heterospecifics (log increase of 0.5, Wald $z = 0.38$, $P = .92$; fig. 6*A*). Accordingly, *S. xerampelinus* spent similar amounts of time near speakers broadcasting conspecific and heterospecific stimuli (70% ± 9% and 73% ± 6%, respectively) compared to controls (32% ± 4%, $F_{2,12} = 11.67$, $P = .001$; fig. 6*B*).

Discussion

Asymmetric patterns of interspecific dominance relative to physiological tolerance are a common phenomenon when ecologically similar species segregate along environmental gradients (e.g., barnacles: Connell 1961; birds: Martin and Martin 2001*b*; bees: Bowers 1985; chipmunks: Heller 1971; Chappell 1978; crayfish: Bovbjerg 1970; fish: Hixon 1980; salamanders: Jaeger 1971*a*, 1971*b*: Griffis and Jaeger 1998). In addition to sharing similar resource requirements, closely related species often overlap in modes of conspecific communication, suggesting that interspecific communication may be a common contributor to ecological processes that define range boundaries. However, few studies have explored how the use of social information contributes to interspecific dominance to mediate spatial segregation. In this study, we aimed to characterize the relative contributions of thermal tolerance and competition to altitudinal zonation in Neotropical singing mice and the role of interspecific communication in mediating competitive exclusion. Across replicate sites, replacement zones were strongly associated with temperature regimes, not altitude; removal experiments indicated that *Scotinomys xerampelinus*, but not *Scotinomys teguina*, is limited by temperature; and field and lab playbacks suggest acoustic communication subserves interspecific dominance of *S. xerampelinus* over *S. teguina*. Our findings suggest that while abiotic regimes circumscribe the location of species replacement, parapatric distributions result from competitive exclusion mediated through asymmetries in interspecific communication. We discuss our findings in relation to interactions between abiotic and biotic factors and highlight interspecific communication in relation to the ecology of social information and its broader relevance in structuring the spatial distribution of animal communities.

Figure 4: Reciprocal removal experiment on Volcán Irazú, Costa Rica. *A*, Average temperature regimes on *Scotinomys xerampelinus* (blue) and *Scotinomys teguina* (red) plots. Shading represents ±1 SE. *B*, Average number of colonizers on control and removal plots for *S. teguina* and *S. xerampelinus*. *C*, Accumulation plot depicting the number of *S. xerampelinus* (blue) colonizing *S. teguina* removal plots as *S. teguina* (red) is removed over time (days). *D*, Accumulation plot depicting the number of *S. teguina* (red) colonizing *S. xerampelinus* removal plots as *S. xerampelinus* (blue) is removed over time (days). Error bars are ±1 SE.

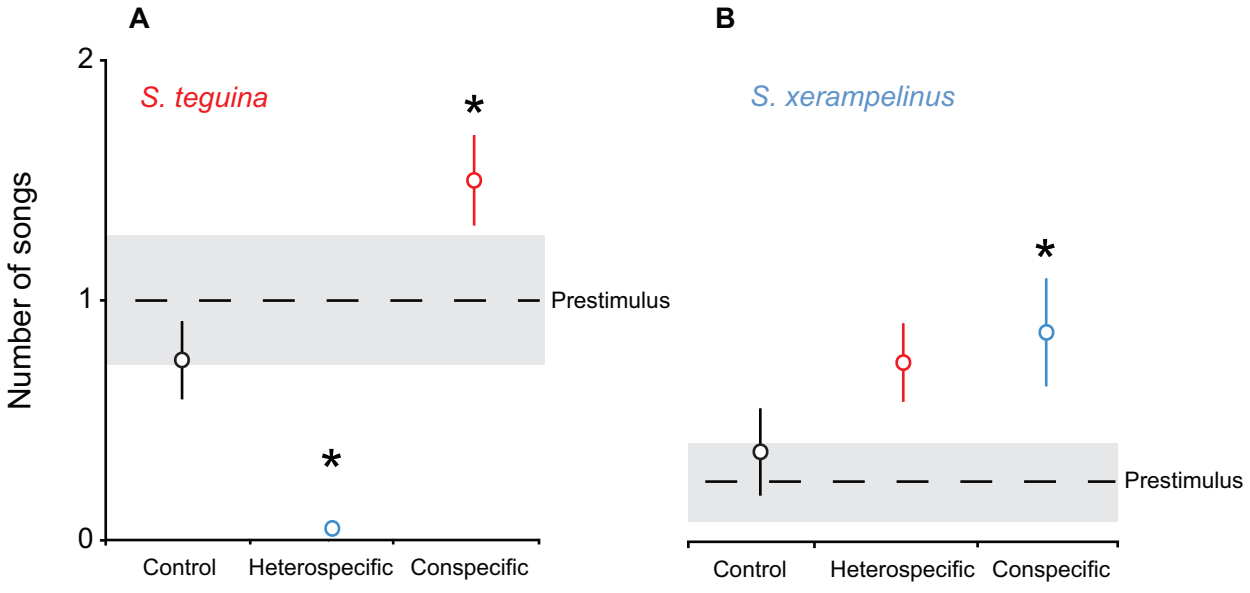


Figure 5: Response to playback trials in the field at Volcán Irazú, Costa Rica. *A*, Number of songs produced by *Scotinomys teguina* (red) to playback of control, conspecific, and heterospecific (blue) stimuli. *B*, Number of songs produced by *Scotinomys xerampelinus* (blue) to playback of control, conspecific, and heterospecific (red) stimuli. Dashed line and shading represents the number of songs produced by focal males prior to playback of stimuli. Error bars are ±1 SE. Asterisk indicates $P < .05$.

Abiotic and Biotic Influences on Altitudinal Replacement

Climate and interspecific competition are posited to be two major factors shaping species range limits in a variety of taxa (Grinnell 1917; Sexton et al. 2009). In the tropics, sharp climatic stratification along mountain slopes is thought to limit species distributions via selection on physiological tolerance to temperature (Janzen 1967; Ghalambor et al. 2006; Tewksbury et al. 2008; McCain 2009). We took advantage of replicate sites of abrupt altitudinal replacement in Neotropical singing mice and asked whether temperature tolerance limited the distribution of either species. While the altitude at which *S. xerampelinus* replaces *S. teguina* differed greatly across study sites, similar temperature regimes at each locality suggested an important role for abiotic factors. At the highest zone of contact (VI), the replacement of *S. teguina* by *S. xerampelinus* coincided with an abrupt transition between two vegetation types. Here, temperature regimes differed substantially across a small spatial scale (fig. 4*A*), where *S. teguina* rapidly colonized cooler *S. xerampelinus* plots, whereas *S. xerampelinus* showed no colonization into warmer, more variable *S. teguina* plots. These data provide evidence that *S. xerampelinus* responds to abiotic conditions and/or other factors that correlate strongly with temperature regimes.

Our findings mirror results of a laboratory study investigating species differences in temperature tolerance (Hill and Hooper 1971). While both species showed thermal tolerances consistent with temperature regimes commonly experienced at native altitudes, experimentally elevating ambient temperatures to 35°C resulted in death of 66% (2 of 3) of *S. xerampelinus* versus 0% (0 of 3) of *S. teguina*. In contrast, only 12.5% (1 of 8) of *S. teguina* and 0% (0 of 7) of *S. xerampelinus* died when ambient temperatures were lowered to 0°–5°C (Hill and Hooper 1971). Despite small sample sizes, the data indicate that *S. teguina* is able to acclimate to a wider range of ambient temperatures. We infer that *S. xerampelinus* is relegated to cold summits, whereas *S. teguina* is less sensitive to prevailing abiotic conditions and can inhabit cooler environments in the absence of dominant competitors.

Although interspecific competition is known to influence species distributions, empirical studies lag behind theoretical models on the extent to which it contributes to evolutionary stable range limits (Case and Taper 2000; Case et al. 2005; Price and Kirkpatrick 2009). Size-dependent interspecific dominance is prevalent in many taxa and may be a common biotic mechanism mediating geographic range limits (Morse 1974; Persson 1985; Glazier and Eckert 2002). In our system, the larger *S. xerampelinus* is behaviorally dominant, as demonstrated by more aggression and shorter latencies to attack in interspecific trials. Moreover, subordinate *S. teguina* exhibited rapid colonization into *S. xerampelinus* removal plots,

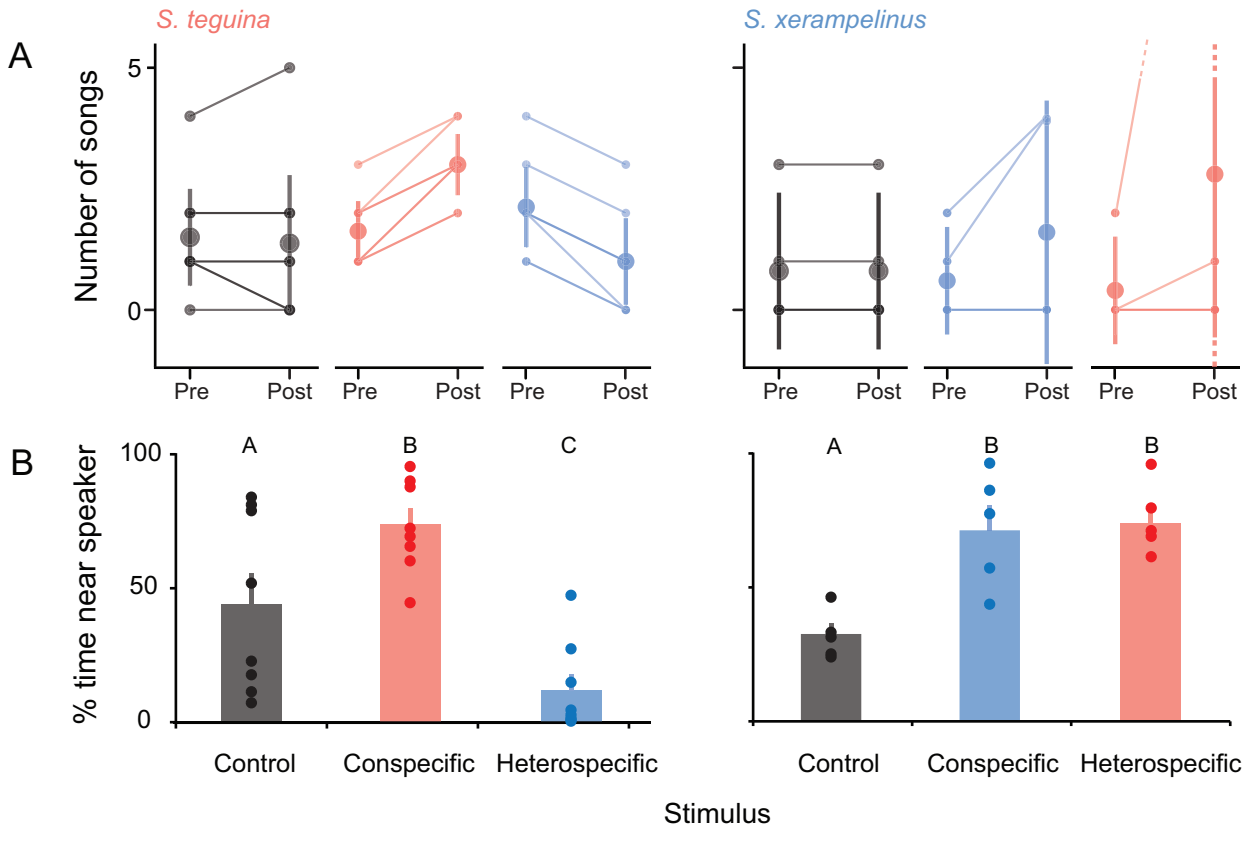


Figure 6: Response to playback trials in the laboratory at Volcán Irazú, Costa Rica. A. Number of songs produced by *Scotinomys teguina* pre- and postplayback of control (black), conspecific, and heterospecific stimuli for *S. teguina* (*left*) and *Scotinomys xerampelinus* (*right*). Darker shapes indicate average ± 1 SE. *B*, Percent time near speaker broadcasting control (black), conspecific, and heterospecific stimuli for *S. teguina* (*left*) and *S. xerampelinus* (*right*). Error bars are ±1 SE. Different letters indicate statistical significance ($P < .05$).

whereas *S. xerampelinus* showed no response to *S. teguina* removal. Such asymmetric interactions suggest that *S. teguina* is limited by interference ("encounter competition"; Schoener 1983) from *S. xerampelinus*, presumably for access to nutrient-rich microenvironments containing larval insects (Hooper and Carleton 1976). Interference competition commonly mediates interspecific dominance among small mammals (Grant 1972; Dickman 1991; Rychlik and Zwolak 2006), where smaller subordinate species tolerate interference because the benefits of gaining temporary access to resource-rich microenvironments outweigh the costs of vigilance and evasion. In contrast, the cost of interference to larger dominant species is low compared to the benefits of exclusive access to prey-rich microenvironments (Chappell 1978; Dickman 1991). Consequently, smaller-bodied species are aggressively repelled by larger-bodied congeners and show rapid competitive release upon their removal (Dickman 1986 *a*, 1986*b*, 1988). Thus, our data suggest that abrupt species range limits emerge from asymmetries in interspecific dominance and are spatially maintained through agonistic interference mechanisms that commonly operate at finer spatial scales (Gotelli et al. 2010).

Interspecific Communication and Its Relevance to Species Distributions

While competitive signaling contributes to intraspecific dominance and spacing, little is known about the role of communication in delimiting spatial distributions between species. In this study, dominant *S. xerampelinus* responded similarly to conspecifics and heterospecifics, whereas subordinate *S. teguina* responded to conspecifics but suppressed singing and avoided heterospecific song. This pattern matches asymmetric dominance interactions observed in the laboratory and competitive release by *S. teguina* in response to *S. xerampelinus* removal in the field.

The response of *S. teguina* to playback of *S. xerampelinus* songs suggests an active avoidance of dominant heterospecifics, presumably to reduce escalation of costly antag-

onistic encounters. Suppression of advertisement displays in situations where conspicuous signals can attract the attention of a potential aggressor is evident in other taxa (McComb and Reby 2005). Whether such avoidance involves associating heterospecific signals with social defeat via auditory learning awaits further experimentation. However, positive response to *S. xerampelinus* songs by *S. teguina* captured 2 km away from the contact zone suggests avoidance behavior is experience dependent (B. Pasch, unpublished data; 2 km is well beyond the ~20-m diameter core areas suggested by telemetry data; Blondel et al. 2009). Regardless, the ability of *S. teguina* to use heterospecific signals to modify approach, avoidance, and vocal behaviors suggests that social information regulates spatial distributions.

The use of information from cues and signals of other species is a widespread phenomenon in animal behavior (Danchin et al. 2004; Dall et al. 2005). Such social information can be used to exploit resources, detect predators, or inform mating decisions (Bonnie and Earley 2007). However, social information can also be important at larger ecological scales to influence processes including habitat selection and community dynamics (Goodale et al. 2010; Schmidt et al. 2010; Parejo et al. 2012). For example, experimental broadcast of avian songs ("social cues") during settlement resulted in a combination of conspecific/heterospecific attraction and heterospecific avoidance, with cascading effects on community composition across the landscape (Fletcher 2006, 2007).

Our data suggest an equally important role of social signals in influencing spatial segregation at species geographical limits. Vocalizations can effectively amplify the rate of behavioral interactions among competing species, thereby facilitating plastic responses to perceived competition. While the trills of singing mice are particularly dramatic examples of social information, the ability of cues and signals to alter behavioral responses among competing species seems likely to be a general phenomenon. For example, trait-mediated interference competition can affect interaction rates among competitors and have important implications for population dynamics (e.g., stabilize simple communities; Bolker et al. 2003). Behavior-based population models that incorporate interspecific communication networks will improve our understanding of coexistence at species limits and provide insight into how large-scale patterns are generated by individual interactions. We suggest that interspecific communication, in its many modalities, is an important yet overlooked mechanism structuring the spatial distribution of communities.

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